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Experimental evidence that grooming and play are social currency in bonobos and chimpanzees

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Abstract

While natural observations show apes use grooming and play as social currency, no experimental manipulations have been carried out to measure the effects of these behaviours on relationship formation in apes. While previous experiments have demonstrated apes quickly learn the identity of individuals who will provide food in a variety of cooperative and non-cooperative situations, no experiment has ever examined how grooming and play might shape the preferences of apes for different individuals. We gave a group bonobos ($N = 25$) and chimpanzees ($N = 30$) a choice between an unfamiliar human who had recently groomed or played with them and one who had not. Both species showed a preference for the unfamiliar human that had interacted with them over the one who did not. The effect was largely driven by the males of both species while interacting with females showed little effect on their preferences for unfamiliar humans. Subjects showed this preference even though they only had social interactions with one of the unfamiliar humans for a few minutes before each trial and their choices were not rewarded with food differentially. Our results support the long held idea that grooming and play act as a form of social currency in great apes (and likely many other species) that can rapidly shape social relationships, particularly between unfamiliar individuals.

Keywords

bonobo, chimpanzee, groom, play, social bonds, social currency.

1. Introduction

Apes, like all primates, rely on social relationships to survive and reproduce. Evidence from several anthropoid species, including chimpanzees, shows that strong individual relationships, both with kin and non-kin, provide adaptive benefits and in many cases are correlated with reproductive

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success (Schülke & Ostner, 2008; Silk et al., 2009, 2010; Gilby et al., 2013). Apes can manipulate social relationships, including through the use of coalitions and alliances to increase rank within the dominance hierarchy (e.g., de Waal, 1982; Goodall, 1986; Surbeck et al., 2011). Social manipulation used to increase rank presumably benefits the individual as rank correlates with measures of fitness (Kano, 1996; Pusey et al., 1997; Gerloff et al., 1999; Boesch et al., 2006; Wroblewski et al., 2009).

Given the importance of social relationships for apes, observational work has been conducted to understand how these relationships are established and maintained. A number of studies in captivity and the wild have shown how bonobos and chimpanzees use grooming to form and maintain social bonds (de Waal, 1982; Kano, 1992). There is evidence for reciprocal grooming in both species (Watts, 2002; Stevens et al., 2006). In chimpanzees there is evidence that male chimpanzees groom their alliance and hunting partners more frequently than non-alliance and hunting partners (Nishida & Hosaka, 1996; Watts, 2000, 2002; Mitani & Watts, 2001). Though bonds between chimpanzees are strongest between male dyads (Gilby & Wrangham, 2008; Mitani, 2009), strong bonds can also form in male–female and female–female dyads (Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009). Meanwhile bonobo mothers and sons seem to preferentially travel together and groom most frequently in the wild (Kano, 1992; Furuichi, 1997; Hohmann et al., 1999; Surbeck et al., 2011). Female bonobos form coalitions to compete against males but strong bonds between males have not been observed (Parish, 1996; Hohmann et al., 1999). Play has also been observed to be another way apes can form and maintain bonds and is important even in adulthood (Goodall, 1986; Palagi et al., 2004; Palagi & Paoli, 2007; Nishida, 2012). Both species tend to play most frequently with kin and allies (Goodall, 1986; Palagi et al., 2004; Nishida, 2012).

Experiments have also been conducted to examine the cognitive abilities in apes that might play a role in relationship formation and maintenance (Tan & Hare, 2013). Bonobos and chimpanzees are both skilled at solving instrumental tasks through cooperation with conspecifics (Melis et al., 2006; Hare et al., 2007). Chimpanzees recruit help when cooperation is necessary and can quickly determine which of two partners is most skillful (Melis et al., 2006). Chimpanzees are able to maintain cooperation when they encounter a conflict of interest through non-verbal negotiation although skills at reciprocity are inconsistent (Melis et al., 2008, 2009; Brosnan et al., 2009). Bonobos retain a more juvenile level of individual tolerance into adulthood that facilitates cooperation in obtaining food, something not seen in chimpanzees (Hare et al., 2007). However, this leads to difficulty in inhibiting previously learned social associations (Wobber et al., 2010a, b). Bonobos also prefer to share food with strange bonobos over groupmates — a preference that may facilitate the extension of social networks in a way not observed in other apes (Hare & Kwetuenda, 2010; Tan & Hare, 2013). A number of experiments have also studied the social preferences of apes using human experimenters. Bonobos and chimpanzees show a preference for a human that was trying to share food with another human over one who was trying to steal the food during a triadic interaction (Russell et al., 2008; Subiaul et al., 2008; Herrmann et al., 2013a). Chimpanzees also demonstrated an almost immediate reversal of preference from a previously stingy to currently generous human in a reversal learning paradigm in which it took them dozens of trials to demonstrate a reversal when a non-social cue like colour was used (Wobber & Hare, 2009). Taken together experimental studies support the idea of bonobos and chimpanzees as flexible cooperators that monitor social relationships closely and rapidly change their preferences — even potentially in interactions with humans.

While observational studies have demonstrated the potential role of grooming and play in social relationships and experiments have shown how flexible bonobos and chimpanzees are in forming and maintaining cooperative relationships, no study has ever experimentally examined grooming and play as a currency in establishing social relationships in apes, where the amount of grooming or other affiliative behavior received leads to a change in preference toward one social partner over the other. While a strong role of grooming and play has long been suspected based on observational work, all previous experimental studies require apes to show social preferences or solve social problems for food rewards (although see Maclean & Hare, 2013). The Social Currency hypothesis suggests that both grooming and play are valued in social interactions and can be used to establish or shift social preferences depending on the amount of play or grooming that occurs between individuals. The central prediction being that an individual can improve their social relationship with another group member by grooming or playing with them. Therefore, an experimental manipulation of grooming and play should show a shift in preference toward those individuals who play and groom subjects the most. If confirmed a secondary question then becomes uncovering the mechanism that might drive such exchanges (e.g., biological markets, Noë & Hammerstein, 1995).

Given the rapid shift in preference for cooperative partners observed in some experiments (Melis et al., 2006; Wobber & Hare, 2009; Herrmann et al., 2013b), it may be apes alter their preferences extremely rapidly based on a relatively short social exchange. In this experiment we will test the social currency hypothesis by manipulating which of two social partners each subject interacts with before choosing which partner they prefer to receive food from. If grooming and play act as social currency, subjects should shift their preference toward an individual that recently played or groomed them. In testing the social currency hypothesis it is also important to examine both *Pan* species since they have very different response to strangers related to establishing new relationships (Tan & Hare, 2013), they handle social stress related to relationship maintenance differently (Wobber et al., 2010a, b), they exhibit temperament differences (Herrmann et al., 2011) and they differ in social cognitive abilities (Herrmann et al., 2010; Wobber et al., 2010a, b). In this context, we predicted bonobos would show greater short-term shifts due to their increased tolerance in general, and especially towards strangers. To control for differences in the two species general preference for interacting with conspecific strangers (i.e., chimpanzees are xenophobic while bonobos are xenophilic), human experimenters were used. When both species have been tested in the same context, they show the same strong preferences to interact with humans over playing alone and neither species has a xenophobic response to humans (Herrmann et al., 2011; Maclean & Hare, 2013).

2. Methods

30 chimpanzees and 24 bonobos housed at the Tchimpounga Centre for Chimpanzee Rehabilitation (Pointe Noire, Republic of Congo) and Lola ya Bonobo (Kinshasa, Democratic Republic of Congo) participated in this experiment. Most subjects arrived at the sanctuary as orphans and have been raised in mixed sex social groups with access to large outdoor forested enclosures where they engage in species-typical behavior including grooming and playing (for details see Wobber & Hare, 2011). Subjects interact with human caretakers on a daily basis when they return to their night dormitories at sunset. Chimpanzees ranged in age from 8–23 years and bonobos from

6–23 years. All had limited exposure to the human experimenters prior to the experimental conditions. A between-subjects design was utilized with 15 chimpanzees and 13 bonobos completing the groom condition and 15 chimpanzees and 12 bonobos completing the play condition (Table 1). Six subjects that were unable to complete the baseline session were dropped from all analyses.

Table 1.
List of subjects.

Chimpanzee				Bonobo			
Subject	Sex	Age	Condition	Subject	Sex	Age	Condition
Elykia	M	22	P	Kikwit	M	14	P
Jo	M	22	P	Lomami	M	12	P
Jay	M	21	P	Illebo	M	10	P
Yoko	M	14	P	Bandaka	M	10	P
Tabonga	M	12	P	Eleke	M	8	P
Chimpie	M	12	P	Yolo	M	8	P
Tiki	M	10	P	Kisantu	F	14	P
Kimenga	M	7	P	Bandundu	F	14	P
Pembele	F	18	P	Likasi	F	10	P
Low-Low	F	18	P	Muanda	F	8	P
Diba	F	15	P	Kinshasa	F	6	P
Fanitouek	F	11	P	Sake	F	6	P
Vitika	F	10	P	Makali	M	25	G
Lounama	F	10	P	Api	M	11	G
Marcelle	F	8	P	Boende	M	11	G
Tomy	M	21	G	Bili	M	10	G
Jacob	M	19	G	Maniema	M	9	G
Tamishi	M	18	G	Kasongo	M	9	G
Tchibanga	M	13	G	Chibombo	M	6	G
Wolo	M	13	G	Isiro	F	14	G
Kefan	M	11	G	Kalena	F	13	G
Petit Prince	M	10	G	Salonga	F	13	G
Lufumbu	M	9	G	Katako	F	7	G
Mayebo	F	22	G	Lukuru	F	6	G
Ramses	F	15	G	Masisi	F	6	G
Ouband	F	11	G				
Oumine	F	11	G				
Ulemvuka	F	10	G				
Makou	F	9	G				
Mvouti	F	8	G				

M, male; F, female; P, play; G, groom.

2.1. Test procedure

The test consisted of two phases and was conducted over 2–3 test sessions. All subjects began with a baseline preference test on day one followed by a test session that was divided across two more days. For a few subjects, the first test session occurred 30 min after the baseline session, rather than the following day, due to management constraints. Care was taken to assure an equal representation of species, sex and condition across the different testing schedules. Three human experimenters (E1, E2 and E3) took part in this experiment. E1 and E2 took part in all preference tests and following the baseline preference test, one was designated as the actor. E3 centred the subject but otherwise did not interact with them in any way. E1 and E2 were unfamiliar individuals though the subjects did have limited experience with them in different capacities. It was not possible to control for gender and race between E1 and E2 (see discussion) due to experimenter availability in the two sanctuaries. Five human experimenters served as E1 and E2 throughout the experiment. KSW was an experimenter for each subject and was known to the apes through minimal exposure during three weeks of study at the sanctuaries a year prior to the current experiment. Upon arrival to complete the current set of experiments, KSW did not interact with the apes prior to testing. At Tchimpounga two caretakers also served as E1 or E2. The primary experimenter was a female caretaker who worked exclusively with the juvenile group, located in a geographically separate area from the sub-adult and adult animals. This caretaker had very limited exposure to the sub-adult and adult individuals. Four older juveniles were tested at Tchimpounga and for these subjects and four additional adults a male caretaker who had a limited role with each group performed the role of second experimenter. At Lola ya Bonobo the second male experimenter was held constant and was only known to the apes through a three-week observational study he had conducted a month prior to the experiment. In this capacity he did not ever have physical contact with the animals and could only observe them from a distance of 10 or more meters. It is important to note that, overall, subjects did not have an a priori preference for one experimenter over the other. KSW served as the actor in 16/30 and 12/24 instances for the chimpanzees and bonobos, respectively.

2.1.1. Baseline

To assess any pre-existing preferences between E1 and E2 apes were given a baseline preference test. Subjects were brought one at a time into a testing room in their night dormitory and were allowed to acclimate to the space. Preference test trials began when E1 and E2 simultaneously gave the subject a slice of banana through the mesh that allowed human–ape interaction, in the centre of the room, before stepping away from the mesh. E3 then re-centered the ape using a banana slice. E1 and E2 stepped forward to the mesh and kneeled, 2 m apart, each holding half a banana in their outstretched hand as E3 stepped away from the testing room. Subjects were allowed to choose to beg from either E1 or E2. Regardless of choice, the subject never received the half banana. This procedure was then repeated for a total of eight trials.

2.1.2. *Test session*

The test session unfolded identically to the baseline preference with the addition of an interaction period during each trial. The actor became the experimenter (E1 or E2) that was least preferred in the baseline session. If the ape showed no preference then the actor was chosen randomly. Trials again began with E1 and E2 giving the subject a banana slice in the centre of the room. The non-actor then remained within arm's reach of the mesh and within a meter of the actor, facing the subject, throughout the interaction period to control for effects of proximity. Crucially, while the non-actor maintained proximity, s/he did not interact with the subject. Simultaneously, the actor began a 3-min interaction period (see below) which varied by condition. Following the interaction period, E3 centred the subject with a small piece of banana and E1 and E2 positioned themselves on either side of the room, counterbalanced by trial, holding half a banana. The subject was allowed to make a choice but was not provided with the banana. Each subject completed 8 test trials.

2.1.3. *Interaction period*

2.1.3.1. Groom condition. The actor sat in front of the mesh and engaged in grooming with the subject by sifting through the hair on the subject's body parts that were within reach of the mesh while making the grooming lipsmack vocalizations. Grooming was not reciprocal and if the subject attempted to groom the actor then the actor shifted positions to widen the space between subject and experimenter. If the subject left the mesh the actor made verbal attempts to call the subject back. Time away from the mesh was coded and included in analysis.

2.1.3.2. Play condition. The actor engaged the subject in high energy play that varied depending on individual preferences. Play could involve ticking, chase and poking and generally included all three. The actor alternated between a cheerful voice and their best attempt to mimic ape laughter vocalizations. If the subject left the mesh the actor made verbal attempts to call the subject back. Time away from the mesh was included in the analysis.

2.2. Coding and analysis

In both baseline and test trials choices were coded live by KSW and 30% of trials were later confirmed through reliability coding using an observer blind to the conditions and hypotheses and Cohen's kappa was 0.958. In the baseline and test trials choice was coded when the subject's fingers crossed the mesh in front of the experimenter. To control for motivation, time spent engaged was coded for each subject. Subjects were free to terminate an interaction with the actor by moving away from the mesh that allows human–ape interaction. Participants were considered engaged if they remained within arm's reach of the mesh barrier. For analysis, we used Poisson regression because the data consisted of counts (number of times the subject picked the actor). Baseline and test observations form repeated measures on the same individual, which are correlated. Generalized estimating equations (GEEs) were used to account for the dependent structure of the data. Inference focused on the treatment variable which had levels baseline and test condition (groom or play). Species, sex of the subject and sex of the human experimenters were included in the model as main effects as well as an interaction terms, condition by species and condition by sex of the subject. These analyses used the geeglm package (Yan, 2002; Yan & Fine, 2004; Højsgaard et al., 2006) in the R environment for statistical computing version 3.1.0 (R Core Team, 2014). An additional model, focusing on males only, was created to test for effects of period (first four vs. last four). Differences in motivation were compared using an independent samples t-test performed in JMP (JMP Pro 10, SAS Institute, Cary, NC, USA). Finally to see if motivation affected choice we ran an ordinary least squares regression on time spent unengaged and the change in preference between the baseline and test conditions, also in JMP.

3. Results

Bonobos increased their preference for the actor in the play condition from 35% in the baseline to 52% in the test session (Figure 1) and in the groom condition from 39% in the baseline condition to 57% in the test condition (Figure 2). Chimpanzees increased their preference for the actor in the play condition from 39% in the baseline to 52% (Figure 1) in the test trials and increased their preference for the actor in the groom condition from 32% in the baseline condition to 47% in the test condition (Figure 2). Species, condition and sex were included in the GEE model as well as interaction effects of species by condition and sex by condition (Table 2). There was no effect of species or experimenter sex but both condition and sex contributed to the model. The effect of sex was entirely driven by males (Figure 1). Males had a coefficient of 0.53 (SE = 0.53, $p < 0.001$) in the groom condition and 0.62 (SE = 0.08, $p < 0.001$) in the play condition. Females had a coefficient of 0.11 (SE = 0.09, $p = 0.25$) in the groom condition and 0.01 (SE = 0.17, $p = 0.96$) in the play condition. A second model (Table 3) that only included males looked at period effect (first four vs. last four). In this model, both groom and play were significant in both periods but the effect size diminished in the last four of the groom condition, indicating subjects were shifting their preference away from the actor in the final half of the session.

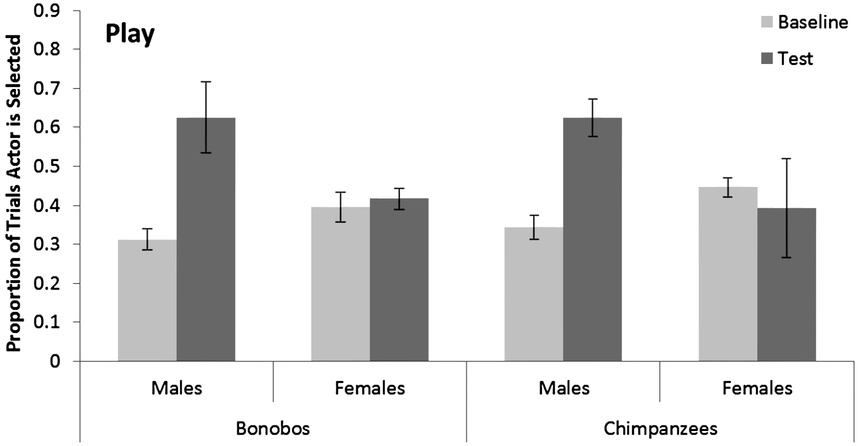

Figure 1. The y-axis represents the proportion of trials the experimenter who groomed the subject or 'actor' was chosen over an experimenter who did not in the baseline (light grey) and test conditions (dark grey) for both species separated by sex in the play condition. Error bars represent standard error.

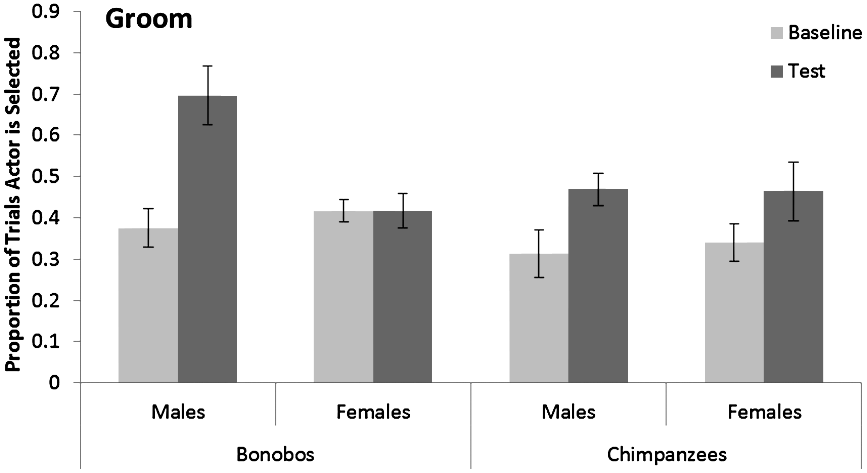

Figure 2. The y-axis represents the proportion of trials the experimenter who groomed the subject or 'actor' was chosen over an experimenter who did not in the baseline (light grey) and test conditions (dark grey) for both species separated by sex in the groom condition. Error bars represent standard error.

Chimpanzees were equally engaged in both conditions ($t = -0.85$, $p = 0.80$), spending 94 and 91% of the time engaged in the play and groom conditions, respectively (i.e., remaining in proximity of the human experimenter). Bonobos were more engaged in the play condition ($t = -2.47$, $p = 0.026$), spending 92% of their time engaged compared to 75% in the groom condition. The level of engagement did not affect the change in pref-

Table 2.
Results of the GEE model.

	Coefficient	p
Species		0.26
Species × Condition		0.05
Experimenter sex		0.20
Males		
Groom	0.53	<0.0001
Play	0.63	<0.0001
Females		
Groom	0.11	0.25
Play	0.01	0.96

Table 3.
Results of the supplementary GEE model, restricted to males but including periods (first four/last four trials).

	Coefficient	p
Period 1		
Groom	0.73	<0.001
Play	0.55	<0.001
Period 2		
Groom	0.31	0.01
Play	0.68	<0.001

erence between the baseline and test conditions (play: $R^2 = 0.05$, $p = 0.29$; groom: $R^2 = 0.06$, $p = 0.20$).

4. Discussion

Chimpanzees and bonobos rapidly changed their preference for a novel experimenter following an affiliative interaction, providing support for the Social Currency hypothesis. Although play and grooming behaviour likely arouse different emotional states in an individual (Rosati & Hare, 2012), apes used both grooming and play interactions equally as a currency to establish social relationships with human experimenters. Bonobos and chimpanzees did not differ in their response to human affiliative behaviors as social currency, despite differences in temperament (Hermann et al., 2011), frequency of cooperative behaviours (Kano, 1992; Muller & Mitani, 2005) and social cognitive abilities (Hermann et al., 2010; Wobber et al., 2010a, b).

The change in preference was strong in both species in both conditions but was primarily driven by males. Female chimpanzees and bonobos did not use play or grooming as a social currency in this particular paradigm. We did not initially predict such a dichotomy, and in fact, would have predicted the sex difference to differ between species due to differential bonding patterns between the sexes (Hohmann et al., 1999; Gilby & Wrangham, 2008). The observed pattern may be related to the shared socioecology between species where females disperse at adolescence (Pusey, 1980; Kano, 1992). In such a system males remain in their natal community for life and gain benefits from forming long-term relationships with kin and non-kin (Hohmann et al., 1999; Mitani, 2009; Surbeck et al., 2011). As males mature, the ability to use affiliative behaviour as a social currency to quickly ascertain the reputation of a partner should hasten the climb up the social ladder given the importance of allies in attaining rank (Nishida & Hosaka, 1996; Surbeck et al., 2011). Males are also likely to benefit from rapidly establishing a rapport with sexually receptive females (Idani, 1991; Kahlenberg et al., 2008). Dispersing females face different social challenges. Increasing evidence shows that females of both species do form differential bonds with both sexes and these relationships are likely to be adaptive (Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009). Moreover, upon immigration females must establish relationships with unfamiliar individuals and should benefit from being able to form reputations based on social currency. Therefore, it is unlikely that females do not use affiliative behaviour as a currency in forming new social interactions. Rather, it may be that females require more time to assess the value of a relationship and our short experimental interactions here are insufficient to see a change in preference. These results are more difficult to interpret in female bonobos. Unlike female chimpanzees who are hostile towards immigrants and less social than males, bonds between bonobo females are generally strong but not long-lasting (Parish, 1996; Hohmann et al., 1999), immigrants seek out specific high ranking females when entering a new community (Idani, 1991) and in experiments both male and female bonobos will pay a cost to have a social interaction with a stranger (Tan & Hare, 2013). These lines of evidence suggest they would show sensitivity to short-term affiliative interactions. Future research comparing these species using conspecific partners or longer periods of interaction may still reveal the expected species difference.

Subjects' rapid shift in preference for a human that either played or groomed with them can best be attributed to the social value of the experimenter's affiliative behaviour. Subjects were not differentially rewarded with food for their choices, making it difficult to explain a shift in preferences during the experiment based on anything but the interaction. Both species interacted with the experimenter similarly, choosing to maintain proximity throughout the interaction period and made choices on every trial. Both experimenters maintained proximity to the subject's room throughout each interaction period. Therefore the shift is not due to a lack of opportunity to interact equally with each experimenter. Although we were not able to hold constant the gender of the experimenters, this did not affect the outcome, primarily because the identity of the actor interacting socially with the subject was determined by selecting the least preferred experimenter for each subject in a baseline. While we observe apes quickly shift preferences based on affiliative interactions, this experiment does not speak to the precise cognitive mechanism involved. Future research will be needed to differentiate between mechanisms such as calculated reciprocity or physiological bonding, increased familiarity or trust through physical contact.

Regardless of mechanism the ability to quickly establish relationships using affiliative behaviors as social currency can have lifelong reproductive consequences for bonobos and chimpanzees. This is especially true for immigrating females who must establish a foraging territory and navigate a new social environment before reproducing (Idani, 1991; Pusey & Schroepfer-Walker, 2013). Females who can integrate more rapidly into their transfer community are expected to have an advantage in early reproduction. Males should also benefit from prioritizing the establishment of certain relationships (Mitani, 2009). As new males mature and move up the hierarchy they can become essential allies for older males and established males should then compete for their attention. They should also be attuned to establishing relationships with females as affiliative relationships may be important for reproductive success. Moreover, cooperation among bonobos and chimpanzees is often predicated on a previously established relationship. The ability to use both grooming and play as a social currency to guide partner choice should lead to stable and strong relationships among individuals.

Here we have established that chimpanzees and bonobos can use play and grooming as a social currency to form relationships. However, with further exploration, we expect to find differences in the speed, the developmental trajectory, the importance of different affiliative behaviours and the point at which social currency is overcome by the accumulation of social debt. We predict that the ability to use affiliative behaviour to form relationships and assess reputation is likely to develop over the juvenile period and should be especially important during the adolescent period when females transfer to their adult communities and males must enter the established hierarchy. Though we did not assess developmental changes, informal observation suggests juveniles and adolescents (10 years and younger) of both species showed larger shifts of preference than adults in the groom condition. Reciprocity is thought to be important for maintaining cooperative interactions in chimpanzees and bonobos. However, despite observational studies that note apes can exchange various commodities, including grooming, meat and coalitionary support (e.g., de Waal, 1997; Koyama et al., 2006; Mitani, 2006; Gomes & Boesch, 2009), experimental evidence is mixed and shows only weak support for contingent reciprocity (Melis et al., 2008; Brosnan et al., 2009). Melis et al. (2008) argue that short-term exchanges may be an inappropriate medium for assessing reciprocity in species that cooperate over long time periods. The current experiment was not designed to specifically address reciprocity but may be helpful in understanding the phenomenon because this experiment assesses interactions between strangers, rather than between individuals with a relationship history. Apes may be willing to pay a higher price in an initial encounter with a stranger to gain information about that individual, even sacrificing food to learn about a new competitor or ally through a social interaction (Hare & Kwetuenda, 2010; Tan & Hare, 2013). However, once the interaction begins, it may behove an individual to watch their accumulation of 'debt'. In this study we found limited evidence that chimpanzees may be attentive to the amount of grooming they receive with no reciprocation across a new interaction. Chimpanzees were less likely to beg from the actor in the latter half of the session (first 4 trials 55%, last 4 trials 38%). This phenomenon was not observed in the play condition (if anything, subjects continued to increase their preference across trials) and suggests grooming may be perceived differently from play in initial short-term interactions. Further work, addressing reciprocity among strangers, should be undertaken to clarify the extent to which apes are capable of contingent reciprocity.

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